

Spitting behaviour of hatchling red spitting cobras (*Naja pallida*)

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Though spitting cobras are able to “spit” their venom even before they fully emerge from the egg, little is known about how this remarkable defensive behaviour is manifest in hatchlings. This study examined three aspects of spitting behaviour in hatchling red spitting cobras (*Naja pallida*) – the amount and dispersal of the spat venom, the kinematics of the head during spitting, and the distance of both the target and the spat venom. Hatchlings spit more venom relative to their body mass than adult snakes, and produce similar patterns of spatial dispersal of the spat venom. Hatchlings exhibit cephalic oscillations during spitting that are similar to those reported in adults, although the magnitudes of these movements are more exaggerated in the hatchlings. The distance covered by the hatchling’s spat venom is much less than that of the adult cobra, and, unlike the adults, the hatchlings routinely spit at targets well beyond their effective spitting range. These results suggest that while the same basic mechanisms underlie spitting in hatchlings and adults, these mechanisms undergo a distinct ontogenetic refinement leading to improved functional performance. Comparisons between the hatchlings and the adults led to the formation of a basic ethological model for venom spitting.

Key words: defensive behaviour, ethology, ontogeny, snake

INTRODUCTION

Venom “spitting” – in which an African or Asian cobra (genera *Hemachatus* and *Naja*) expels venom from their fangs towards the eyes of a potential predator – is one of the most specialized and dramatic defensive behaviours in snakes. These snakes have been the focus of our research for several years, but our work, like almost all of the literature on these taxa, was based exclusively on analyses of late juvenile or adult specimens. The small size and (presumed) lower musculo-skeletal coordination of early hatchlings suggest that key features of this behaviour may change significantly during ontogeny.

The expulsion of venom during spitting is based on a two-stage mechanism of muscle contraction (Young et al., 2004). In adult cobras coordination of these muscles produces relatively consistent volumes of spat venom (Young & O’Shea, 2005) equal to roughly 2% of the total venom gland volume in each spit (Cascardi et al., 1999). Given the allometrics of venom yield (McCue, 2006) and the refinement of neuromuscular coordination during ontogeny (e.g. Muir, 2000), our first hypothesis is that hatchling cobras would exhibit a different pattern of spat venom volume.

Adult *Naja pallida* can spit venom for distances of roughly two metres (Rasmussen et al., 1995). Spitting cobras appear to be able to judge the distance of their target; they vary the trajectory of their spit depending on target distance (Berthé et al., 2009) and will very rarely spit at a target that is beyond the effective range of their spitting mechanics (Westhoff et al., 2005). Our second hypothesis is that naive hatchlings will not exhibit such marked con-

trol over the spatial features of spitting, whether due to inefficiency in gauging distances, their greater sensitivity to potentially threatening encounters, or the allometrics and ontogenetic coordination of the functional basis of spitting.

In adult cobras venom spitting is always associated with rapid oscillations of the head (Young et al., 2004; Westhoff et al., 2005). These angular displacements of the skull – produced by contraction of the axial musculature – impart spatial patterns to the spat venom that have been interpreted as a way of maximizing the chance of the venom contacting the corneal surface (Young et al., 2008). Our third hypothesis is that hatchling cobras will exhibit similar distinctive spatial patterns to the spat venom, albeit perhaps with more distinctive cephalic rotations.

MATERIALS AND METHODS

Live animals

A clutch of 28 eggs from *N. pallida* were incubated on a mixture of vermiculite and sphagnum in sealed plastic containers with small holes for ventilation. The eggs were incubated at 29 °C and inspected every other day. Once slits appeared in the eggs the behaviours of the hatchlings were observed more frequently. The egg clutch produced a total of 19 hatchlings, which were transferred, in groups of two, into ventilated cages (35 × 23 × 14 cm) within 36 hours of hatching. The experiments reported herein were initiated immediately upon hatching, extended through first ecdysis (4–5 days post-hatching), and for approximately three days after the first ecdysis. Observations were also made on a second clutch of *N.*



Fig. 1. Planar distribution of venom spat by hatchling *Naja pallida*. A) A linear distribution in which the venom ejected by both fangs remains distinct; B) a uniform distribution in which the contribution of each fang cannot be discerned.

pallida that hatched approximately one week later. All protocols were in compliance with the applicable standards for the care of and experimentation with live vertebrates.

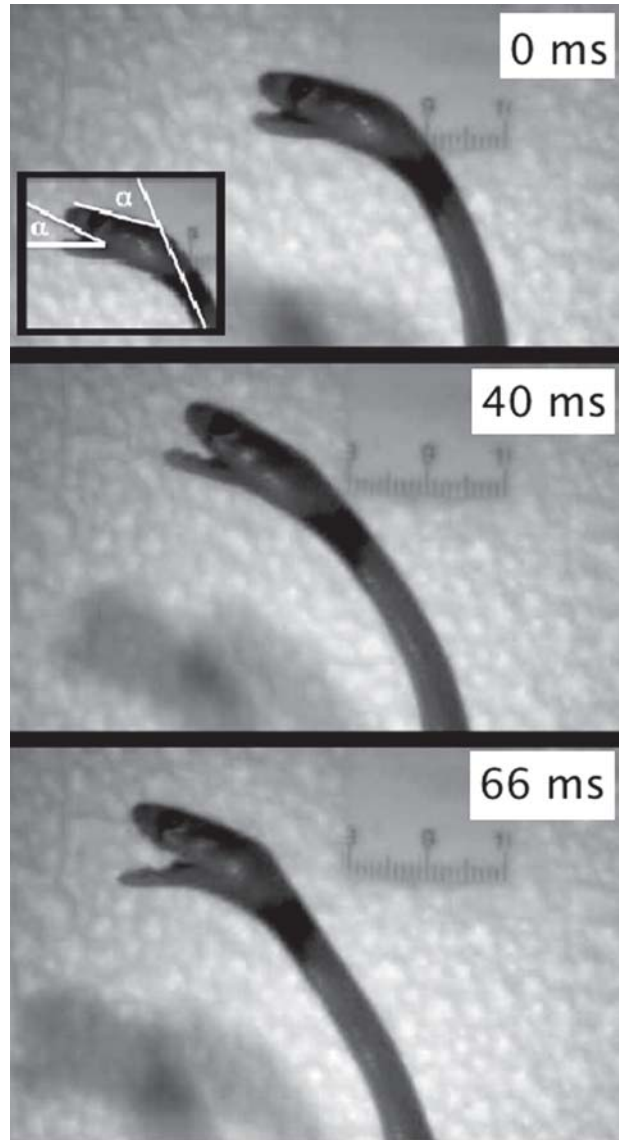


Fig. 2. Three isolated frames from a high-speed (500 fps) digital video record of venom spitting in a hatchling *Naja pallida*. Note the changes in both the dorsal head angle (the angle between the dorsal surface of the skull and the midline of the long axis of the neck) and the gape angle (the angle between the oral margins of the upper and lower jaws) during venom expulsion. Numbers in the frames represent millisecond durations.

Spat venom

The young snakes were placed individually in a plastic container (35 × 23 × 14 cm) with no lid. The cobras were approached by one of the authors who held a 21 × 15 cm acetate sheet in front of his/her face. The spat venom was caught on the acetate sheet; the venom dries almost instantly allowing the spatial pattern of the venom to be photographed digitally. To determine the mass of venom spat the acetate sheets, along with the captured venom, were weighed the next day using an XS-310D digital balance (Denver Instruments; sensitivity 1 mg). ImageJ (N.I.H.) was used to quantify the area of the acetate sheet

Table 1. Cephalic movements of hatchling *Naja pallida* during venom spitting ($n=12$). Range of head angle is the difference between the maximal and minimal angle observed during the oscillations of the head around the neck. Range of gape angle is the difference between the maximal and minimal angle formed between the upper and lower jaws. Temporal offset is the time between the maximal head angle and the maximal gape.

	Mean	S.D.	Range
Head rotation about neck (degrees)	19.1	6.1	7–34
Change in gape angle (degrees)	9.6	4.8	1–20
Time (msec) from max head rotation to max gape angle	41.5	27.7	-28–86

which, when compared to control sheets with no spit, enabled the calculation of the dried mass of the spat venom. Following venom collection the hatchlings were gently tubed and their snout–vent length (SVL) determined. The cobras were then weighed using a ScoutII digital balance (Ohaus Corp., Pine Brook).

Spitting kinematics

A small (20 cm tall \times 20 cm wide \times 30 cm deep) filming cage was constructed with an open front and a side of glass. A Troubleshooter 500S camera (Motion Engineering) was used to film the cobras at 500 fps. The digital output from the camera was streamed to a PC laptop running CameraLink software (Motion Engineering). Illumination for filming was provided by a 200W light (Lowel Pro). The displacements of the head and lower jaw during spitting were quantified using ImageJ (N.I.H.).

Spitting performance

The hatchlings were placed in the same filming cage described above, and the cage was placed atop a 50 cm high table within a long hallway. A 25 \times 120 cm glass plate was placed on a second 50 cm high table and positioned so that it abutted the front of the filming cage then extended down the hallway. A measuring tape was placed along the length of this glass plate, and additional 10 cm increments were placed on the floor extending away from the far end of the glass plate an additional 150 cm. The hatchlings were placed in the filming cage and induced to spit by the presence and motions of one of the authors. As soon as the cobra spat the distance of the “target” was recorded and the filming cage covered with a thick cloth to visually isolate the snake. The spat venom droplets were readily observable on the glass plate. The maximal distance covered by the spat venom was recorded, and the glass plate washed and dried of venom. Special care was taken to note the presence of “sham” spits – in which the cobra displayed all the kinematic features of a spitting episode

but no venom was expelled – and the inclination of the cobra to spit multiple times.

RESULTS

Spitting behaviour

The hatchling *N. pallida* spat even before fully emerging from the egg. These cobras would often remain for an extended period (in some cases more than 24 hours) with only their head protruding through the slit in the egg; while in this position the hatchlings would spit repeatedly. In the first few days after emerging the cobras spat repeatedly and seemingly with little target discrimination; the hatchlings regularly spat at one another but would also spit at stationary objects such as other eggs and the side of their cage. The appearance of one of the authors would trigger spitting behaviour in many of the hatchlings, and the responding hatchlings were then targeted by several of the initially unresponsive cobras. This apparently non-selective spitting continued through the first ecdysis (approximately 4–5 days post-hatching). The incidence of spitting decreased markedly after the first ecdysis, and target specificity appeared to increase. Post-ecdysis we did not observe the cobras spitting at inanimate objects and only rarely saw a hatchling spit at a cohort member.

Spat venom

A total of 14 venom spats of *N. pallida* were caught on the acetate sheets. There was considerable variation in the planar distribution of this spat venom. In 11 of the 14 (79%) caught spats, the planar venom distribution had a distinctly linear component in which the venom streams discharged by the two fangs remained distinct (Fig. 1A). In the remaining three of the 14 caught spats (21%), the venom formed a relatively uniform distribution of venom droplets in a roughly ovate shape (Fig. 1B).

The dried mass of this caught spat venom ranged from 6 to 23 mg with a mean of 14.6 (S.D.=4.2). We used a constant conversion factor of $\times 2.5$ to estimate wet venom mass (see Mirtschin et al., 2006), though we recognize that this conversion factor can be influenced by many variables (Mirtschin et al., 2002). These hatchling cobras had body masses of 13.6–16.2 g, with a mean of 15 g (S.D.=0.67). As such, the venom we gathered from single spits ranged from 0.09 to 0.43 % of the cobras’ total body mass (mean = 0.24%).

Spitting kinematics

A total of 12 spitting episodes were captured on high-speed digital video. Each of these spits was characterized by oscillatory displacements of both the head relative to the neck, and the lower jaw relative to the head, during the expulsion of the venom (Fig. 2). The gape angle formed between the upper and lower jaws changed less than did the angle formed between the dorsal surface of the skull and neck (Table 1). The most variable feature of these oscillations was the relative timing of these two displacements; in some cases maximal gape preceded maximal head elevation (expressed in Table 1 as a negative value), though most commonly the changes in gape angle trailed the oscillations of the head (Table 1).

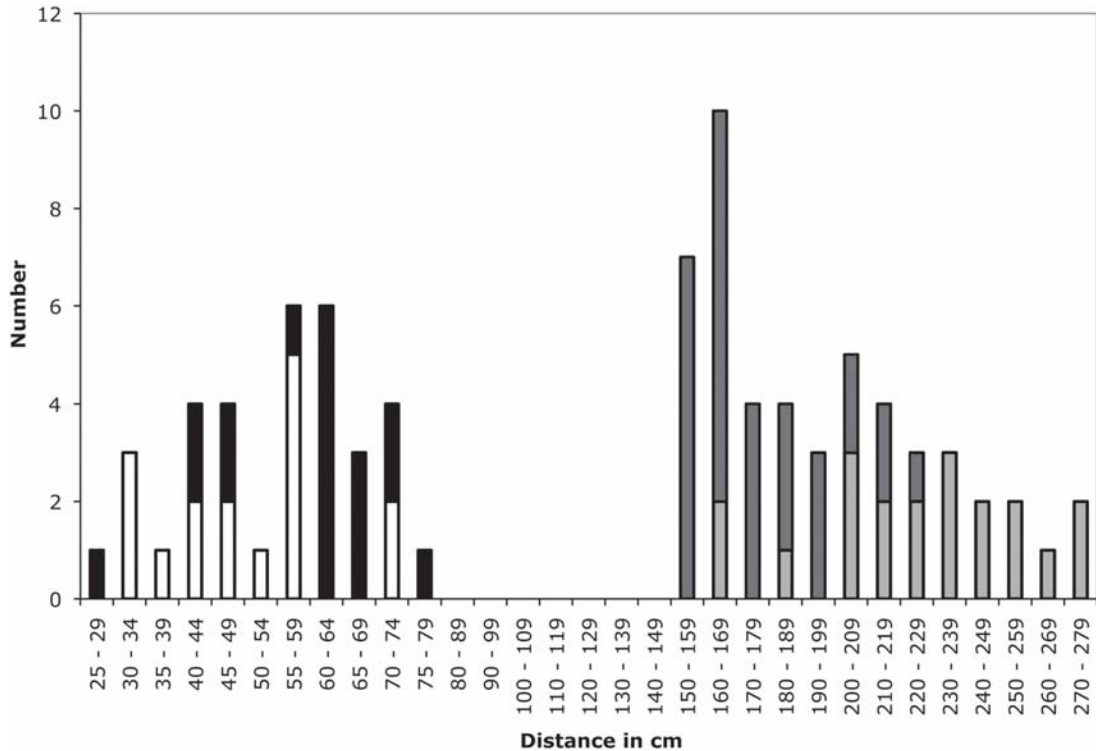


Fig. 3. Spitting performance of hatchling *Naja pallida*. (Left): open boxes – distance covered by the venom spat by pre-ecdysis hatchlings; black boxes – distance covered by the venom spat by post-ecdysis hatchlings. (Right): light grey boxes – distance to target when the pre-ecdysis hatchlings spat; dark grey boxes – distance to target when the post-ecdysis hatchlings spat. Note the marked discrepancy between target distance and the distance covered by the spat venom, and the reduction in this discrepancy after ecdysis.

Spitting performance

When the measured distances are expressed as line of sight distance, the mean distance to induce a spit was 196 cm (S.D.=12.7 cm, $n=50$) and the mean distance traveled by the venom was 54.8 cm (S.D.=4.6 cm, $n=34$). The different sample sizes (50 versus 34) reflect that in 16 of the trials the hatchlings responded to the stimulus by performing sham spits in which no venom was released. The gap between target distance and spitting distance narrowed after the first ecdysis. Twenty of the spitting performance trials were conducted prior to the first ecdysis: in these trials the mean target distance was 225.2 cm (S.D.=19.8) and the mean distance traveled by the venom was 49.6 cm (S.D.=8.4) (Fig. 3). Thirty trials were conducted on the same cohort after ecdysis: in these trials the mean target distance was 176.7 cm (S.D.=10.2) while the mean distance traveled by the venom was 59.4 cm (S.D.=8.7) (Fig. 3). A Wilcoxon signed test revealed that post-ecdysis the target distance was significantly less ($W=3.219$, $P<0.01$), while the distance travelled by the spat venom was significantly greater ($W=2.14$, $P=0.043$).

No more than five trials were conducted with a single hatchling. Pooling the pre- and post-ecdysis trials, and ignoring any trial in which the hatchling performed a sham spit, we had trials for nine specimens in which the cobra performed at least three spits. There is no evidence of habituation or any other alteration in spitting performance across these trials (Table 2). Using the Wilcoxon

signed test, neither the distance to target ($P=0.64$) nor the distance travelled by the spat venom ($P=0.87$) were significantly different between the first and third trial.

DISCUSSION

This study was undertaken to test three hypotheses concerning venom spitting in hatchling *N. pallida*: 1) that hatchling cobras would exhibit a different pattern of spat venom volume than adults; 2) that naive hatchlings would not exhibit such marked control over the spatial features of spitting as adults do; and 3) that hatchling cobras would exhibit distinctive spatial patterns to the spat venom that are similar to those seen from adults.

Previous studies have remarked that the volume of venom spat by a particular species of cobra is fairly consistent (Freyvogel & Honegger, 1965; Cascardi et al., 1999; Young & O’Shea, 2005). An earlier study (Cascardi et al., 1999) claimed that adult *N. pallida* spit approximately 2% of the volume of their venom gland with each spit; this percentage would explain the frequent observation that cobras can spit multiple times before becoming “dry” (e.g. Sweeney, 1971; Spawls & Branch, 1995; Cascardi et al., 1999; Trutnau & Stremme, 2004). In contrast, the caught spats from the hatchling *N. pallida* had a mean wet mass (36.5 mg) equal to 0.24% of their mean entire body mass (14.98 g). If these hatchlings were performing 50 equal spits (50 consecutive spits have been reported from adult *N. pallida*), they would lose over 12%

Table 2. Variation in spitting performance across trials ($n=34$). The results of the first three (non-sham) trials are shown after pooling pre- and post-ecdysis data. Note the rather consistent performance, in terms of both target distance and distance covered by the spit, among these trials.

	Target distance	Venom distance
First trial	195.1 (34.0)	57.6 (15.5)
Second trial	199.3 (37.4)	56.9 (17.4)
Third trial	201.9 (56.6)	57.0 (16.7)

of their body mass. While we have not quantified the volume of venom held in a hatchling cobra's venom gland, these numbers strongly suggest that hatchling *N. pallida* are spitting proportionately more venom than adults. While different methodologies were employed, the mean dry mass of spat venom found in this study (14.6 mg) is roughly 4.5 times that determined from adult *N. pallida* (Cascardi et al., 1999). This greater volume of venom being spat might represent a form of compensatory mechanism by which a young cobra ensures that enough venom is discharged to make contact with the corneal surface of the predator. Alternatively, these hatchling snakes may not have such fine neural control over the skeletal muscle that forms the propulsive force for the spat motive (Young et al., 2004). In either case, our findings support our hypothesis that hatchling cobras exhibit a different pattern of spat venom volume than adults.

The venom that is spat has a planar distribution characterized by distinct right and left dispersals typically showing a clear geometric pattern (Fig. 1). Similar spatial distributions of spat venom have been reported from laboratory and field studies of cobras, including *N. pallida* (e.g., Westhoff et al., 2005; Young & O'Shea, 2005; Young et al., 2008). These results support our hypothesis that the distinctive spatial patterns to the spat venom would be similar in adult and hatchling cobras.

An earlier study of adult *N. pallida* (Young et al., 2008) reported that the spatial dispersal of the spat venom was produced by rapid oscillations of the cobra's head during venom expulsion. High-speed videographic analysis demonstrates that hatchling *N. pallida* exhibit the same type of cephalic rotation during spitting (Fig. 2). The presence of the same basic kinematic displacements during spitting in hatchling and adult snakes suggests that they are using the same underlying mechanics for venom expulsion (Young et al., 2004). While the basic kinematic patterns are similar, the rotations (of both the head relative to the neck, and the lower jaw relative to the head) are more pronounced in the hatchling. These cephalic oscillations have been interpreted as a mechanism to increase the probability of the spat venom contacting the target's cornea (Young et al., 2008); we hypothesize that the decrease in the range of kinematic oscillations during ontogeny may reflect maturation within the neuromuscular system (either in terms of targeting or motor control).

What makes the cephalic oscillations of these hatchlings particularly interesting is that they were performed while the snake was spitting at targets that were well beyond the effective range of their spat venom (Fig. 3). Adult *N. pallida* effectively compensate for distance, making smaller cephalic oscillations with increasing target distance; this compensation keeps the venom dispersal to a relatively constant area roughly equivalent to the target's eye width (Westhoff et al., 2005; Berthé et al., 2009). Hatchling *N. pallida* do not exhibit this compensation; while spitting at distant targets they use larger oscillations than even the adults perform for close targets.

There is a substantial difference in the distance covered by the spat venom of adult and hatchling cobras. The mean distance covered by the spat venom of hatchlings (54.8 cm) is roughly one-quarter of the distance at which adult *N. pallida* can hit a target (Rasmussen et al., 1995). There is considerable interspecific variation in the distance covered by the spat venom of cobras (Rasmussen et al., 1995). Despite this variation, there is a common behavioural attribute: adult spitting cobras are reluctant to spit at a target that is outside their effective spitting range (Westhoff et al., 2005). This is clearly not the case with hatchlings: in every spitting trial we conducted, the hatchling *N. pallida* spat at a target well outside their spitting range (frequently the target was roughly four times the distance of the venom range; Fig. 3). These results support the idea that naive hatchlings will not exhibit such marked control over the spatial features of spitting as adults do. Some variation in target distance could be attributable to differences in the height of the (moving) target, and variation in the angle at which the venom was spat; none of this potential variation could account for the marked disparity between target distance and effective spitting range.

The motive force used to propel the venom through the air comes from the skeletal muscle surrounding the venom gland (Freyvogel & Honegger, 1965; Young et al., 2004); the difference in spitting range presumably reflects the physiological development of this neuromuscular system. Other studies of vertebrate neuromuscular ontogeny have shown similar improvements within time periods of a few weeks (e.g. Seelke et al., 2005; van Wessel et al., 2005). This interpretation is supported by the finding of significant improvements in spitting performance (in terms of increased spitting range and reduced target distance) following ecdysis, which is an early marker of ontogeny in snakes.

Ethological model of spitting

Adult spitting cobras only spit when the provocation or threat produces a threshold level of arousal (Fig. 4A). Below this level of arousal, adult cobras exhibit a range of other defensive behaviours including crypsis, fleeing and hooding (e.g. Carpenter & Ferguson, 1977). Too much provocation or threat, which is to say excessive arousal, also diminishes spitting behaviour. When overly stimulated spitting cobras will frequently stop spitting and simply lunge and bite, or may feign death (e.g. Spawls & Branch, 1995). The relationship between arousal and the tendency to spit in adult cobras is interspecifically vari-

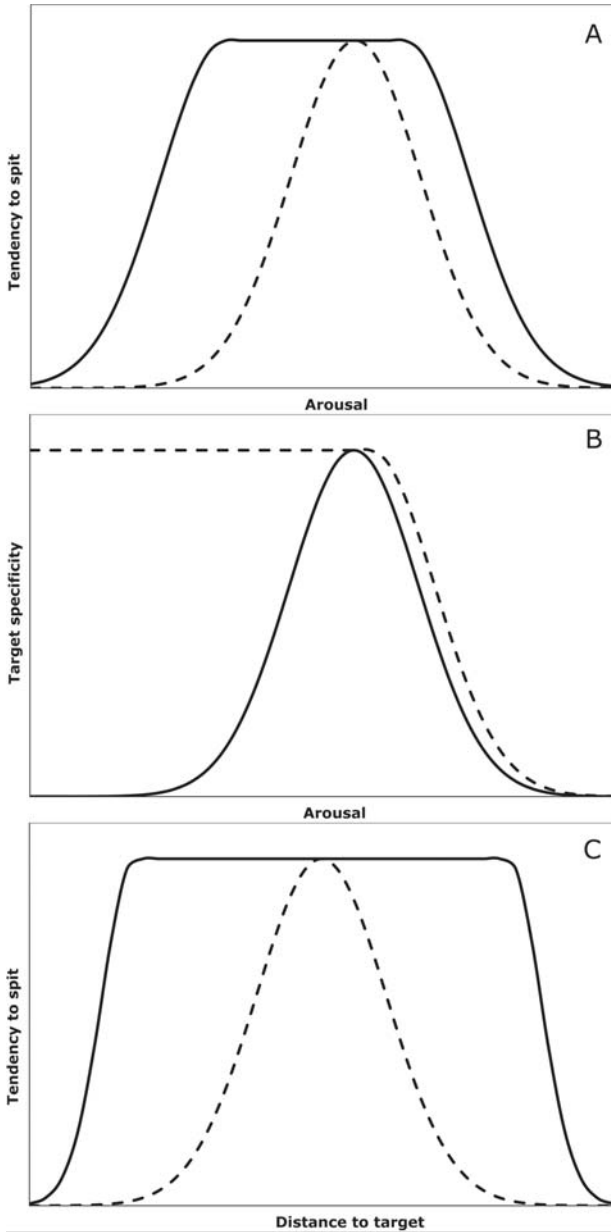


Fig. 4. Generalized model for the ethology of spitting in cobras. A) Hypothetical response curves relating increased arousal (x-axis) to tendency to spit (y-axis); B) hypothetical response curves relating increased arousal (x-axis) to target (eye/face) specificity (y-axis); C) hypothetical response curves relating increased distance to target (x-axis) to tendency to spit (y-axis). The dashed curve represents a generalized adult spitting cobra while the solid curve represents a generalized hatchling.

able; in our experience *N. siamensis* will spit with less arousal than most other cobras, while *Hemachatus hemachatus*, for example, spits at higher levels of arousal (presumably due to the pronounced death feigning in this species; unpublished observations). Our observations suggest that the relationship between arousal and the tendency to spit is much broader in hatchling cobras (Fig. 4A); it requires far less arousal to get a hatchling cobra to

spit and they continue to spit at higher levels of arousal. This may reflect the relative paucity of other defensive behaviours available, or that, given the small size and relative fragility of hatchlings, every encounter results in high levels of arousal.

A closely related difference between adult and hatchling spitting cobras is that at lower levels of arousal adult spitting cobras have a high target specificity (Fig. 4B). The first spit from an adult spitting cobra is almost always directed at the eyes/face of the threat (Rasmussen et al., 1995; Westhoff et al., 2005). With increasing arousal the target specificity will eventually decline. In our experience highly agitated adult spitting cobras will spit at almost any moving object and will often spit at stationary inanimate objects (especially mirrors or other reflective surfaces). This target specificity is largely lacking in hatchling spitting cobras, particularly at low levels of arousal (Fig. 4B). As described above, we have repeatedly observed hatchling cobras spitting at their cohort members, at unhatched eggs, and even at the sides and lids of their cages. With increased provocation, such as the presence of one of the authors, the hatchlings seemed more “focused” and often seemed to be trying to spit at the nearest author’s head. Nevertheless, they could easily be induced to spit at a moving hand or inanimate object.

One other distinct difference between adult and hatchling spitting cobras is how this behaviour is influenced by target distance (Fig. 4C). Adult spitting cobras will rarely spit at a target that is close enough to bite, and will almost never spit at a target that is outside the range of its spat venom (Westhoff et al., 2005). As detailed above, the hatchling cobras will spit over a considerable range of target distances (Fig. 4C), including those far in excess of their effective spitting range. Our experience suggests that the upper limit to spitting in hatchling cobras is determined primarily by the acuity of their sensory (particularly visual) systems. In contrast, an adult spitting cobra will remain stationary and follow a target’s movements (suggesting that adequate visual stimuli are being received) until the target is close enough, at which time the cobra will spit with no additional defensive behaviour.

We hypothesize that the differences in venom spitting behaviour in hatchling cobras – the higher inclination to spit and the lower target specificity – may be a mechanism to exercise or fine-tune the neuromuscular basis of spitting (Young et al., 2004). The tendency of a hatchling spitting cobra to expel venom at cohorts and inanimate objects is clearly “wasteful” in terms of venom energetics, particularly given the proportionately large amounts of venom spat. Nevertheless, this early period of (almost) random spitting would be advantageous if it resulted in improved performance that could increase the likelihood of a young cobra surviving an encounter with a predator. The distance covered by the spat venom of *N. pallida* showed significant improvement over a roughly one-week interval on either side of the first ecdysis (Fig. 3). Presumably this early period of improved neuromuscular performance would be followed by a longer period during which the spitting performance increased due to allometric increase in force output in the propulsive muscle surrounding the venom gland.

Some ophidian defensive behaviours are only rarely seen in newborn individuals (e.g. death feigning, or aposematic tongue flicking in rattlesnakes). In contrast, venom spitting in cobras is almost exaggerated in hatchlings, both in terms of inclination to spit and relative volume of spat venom. There may be some unusual aspects to the behavioural ecology of cobras that place their hatchlings at relatively greater risk than the adults; for example, Spawls & Branch (1995) note that in some cobras the juveniles are more diurnal than the adults. It seems more likely that the heightened propensity for spitting in hatchling cobras is predominantly a mechanism whereby the performance of this system is improved.

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REFERENCES

- Berthé, R.A., de Pury, S., Bleckmann, H. & Westhoff, G. (2009). Spitting cobras adjust their venom distribution to target distance. *Journal of Comparative Physiology A* 195, 753–757.
- Carpenter, C. & Ferguson, G. (1977). Variation and evolution of stereotyped behavior in reptiles. In *Biology of the Reptilia*, Vol. 7, 335–554. Gans, C. & Tinkle, D. (eds). New York: Academic Press.
- Cascardi, J., Young, B.A., Husic, D. & Sherma, J. (1999). Protein variation in the venom spat by the pink spitting cobra (*Naja pallida*) (Reptilia: Serpentes). *Toxicon* 37, 1271–1279.
- Freyvogel, T. & Honegger, C. (1965). Der ‘Speiakt’ von *Naja nigricollis*. *Acta Tropica* 22, 289–302.
- McCue, M.D. (2006). Cost of producing venom in three north American plover species. *Copeia* 2006, 818–825.
- Mirtschin, P.J., Shine, R., Nais, T.J., Dunstan, N.L., Hough, B.J. & Mirtschin, M. (2002). Influences on venom yield in Australian tigersnakes (*Notechis scutatus*) and brownsnakes (*Pseudonaja textilis*: Elapidae, Serpentes). *Toxicon* 40, 1581–1592.
- Mirtschin, P.J., Dunstan, N., Hough, B., Hamilton, E., Klein, S., Lucas, J., Millar, D., Madars, F. & Nais, T. (2006). Venom yields from Australian and some other snake species. *Ecotoxicology* 15, 531–538.
- Muir, G.D. (2000). Early ontogeny of locomotor behaviour: a comparison between altricial and precocial animals. *Brain Research Bulletin* 53, 719–726.
- Rasmussen, S., Young, B.A., & Krimm, H. (1995). On the “spitting” behavior in cobras. *Journal of Zoology* 237, 27–36.
- Seelke, A., Karisson, K., Gall, A. & Blumberg, M. (2005). Extraocular muscle activity, rapid eye movements and the development of active and quiet sleep. *European Journal of Neuroscience* 22, 911–920.
- Spawls, S. & Branch, B. (1995). *The Dangerous Snakes of Africa*. London: Blandford.
- Sweeney, R.C.H. (1971). *Snakes of Nyasaland*. Amsterdam: A. Asher & Co.
- Trutnau, L. & Stremme, D.W. (2004). *Venomous Snakes: Snakes in the Terrarium*. Florida: Krieger.
- Van Wessel, T., Langenbach, G., Brugman, P. & Eijden, T. (2005). Long-term registration of daily jaw muscle activity in juvenile rabbits. *Experimental Brain Research* 162, 315–323.
- Westhoff, G., Tzschätzsch, K. & Bleckmann, H. (2005). The spitting behavior of two species of spitting cobras. *Journal of Comparative Physiology A* 191, 873–881.
- Young, B.A. & O’Shea, M. (2005). Analyses of venom spitting in African cobras (Elapidae: Serpentes). *African Zoology* 40, 71–76.
- Young, B.A., Dunlap, K., Koenig, K. & Singer, M. (2004). The buccal buckle: the functional morphology of venom spitting in cobras. *Journal of Experimental Biology* 207, 3483–3494.
- Young, B.A., Boetig, M. & Westhoff, G. (2008). The functional bases of the spatial dispersal of venom during cobra “spitting”. *Physiological and Biochemical Zoology* 82, 80–89.

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